TETHYOCHONETES GEN. NOV. (CHONETIDA, BRACHIOPODA) FROM THE LOPINGIAN (LATE PERMIAN) OF CHINA

Z. Q. Chen, G. R. Shi, Shuzhong Shen & N. W. Archbold

School of Ecology & Environment, Deakin University, Rusden Campus, 662 Blackburn Road, Clayton, Victoria 3168, Australia

Chen, Z. Q., Shi, G. R., Shen Shuzhong & Archbold, N. W., 2000:06:30. *Tethyochonetes* gen. nov. (Chonetida, Brachiopoda) from the Lopingian (Late Permian) of China. *Proceedings of the Royal Society of Victoria* 112(1): 1–15. ISSN 0035-9211.

A new rugosochonetid genus, *Tethyochonetes* gen. nov., is proposed for several species from the Lopingian (Late Permian) of China previously assigned to *Waagenites* Paeckelmann, 1930. Five species of *Tethyochonetes* are described, including two new species, *Tethyochonetes? liaoi* sp. nov. and *Tethyochonetes chaoi* sp. nov., and three revised species, *Tethyochonetes quadrata* (Zhan), *Tethyochonetes longtanensis* (Liao) and *Tethyochonetes wongiania* (Chao).

WAAGENITES Paeckelmann, 1930, with *Chonetes grandicosta* Waagen (1884) as the type species, was proposed without a description of dorsal internal features. *Waagenites* has subsequently been widely applied to numerous species showing a variety of morphological features (Muir-Wood 1962, 1965; Waterhouse & Piyasin 1970; Grant 1976). The generic name has been widely applied to many chonetid specimens from the Late Permian (Wuchiapingian and Changhsingian) of China. Some authors have noted distinct differences between these species and the type species (Waterhouse & Piyasin 1970; Grant 1976; Liao 1979: 200, 1987: 99; Zhan 1979: 71; Xu 1987: 119–220; Zeng et al. 1995: 48–49). In this study, we re-examine several of these Chinese species and compare them with published information of *Waagenites grandicosta* (Waagen) and *Waagenites* species from western Yunnan. We note distinct differences between the Late Permian Chinese species and *Waagenites grandicosta* and its allied species, and therefore propose *Tethyochonetes* gen. nov. for the Late Permian Chinese species.

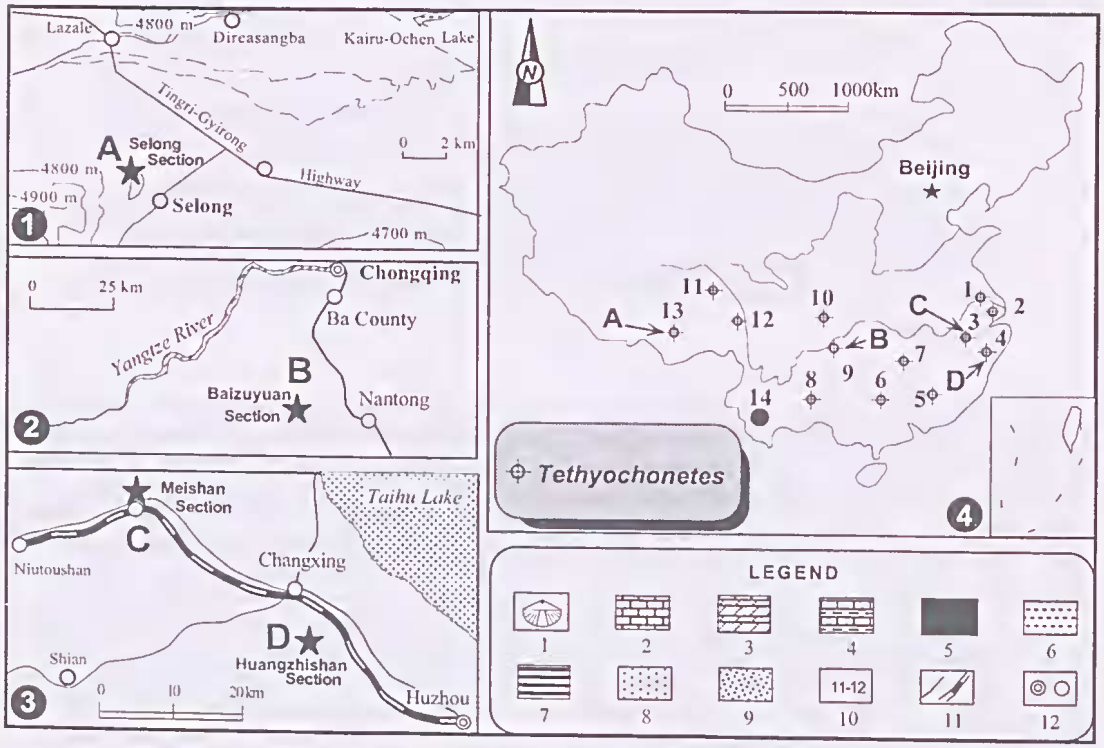
All described material is deposited in the following institutions: the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences, China (NIGP); and Museum Victoria, Melbourne, Australia (NMV).

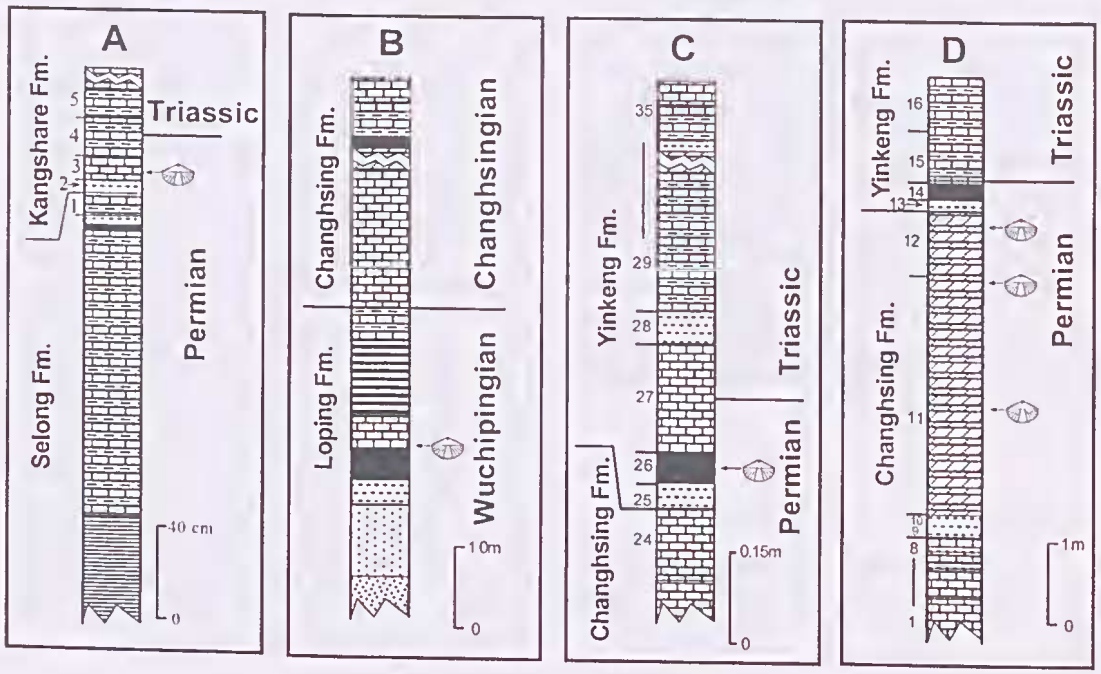
STRATIGRAPHY OF THE NEW MATERIAL

The described specimens were collected from four sections within Late Permian sequences of China (Fig. 1). The sequence across the Permian–Triassic boundary in the Selong section (Section A, Fig. 1) of Nyalam County, southern Tibet, has been subdivided into five informal lithological units, namely (in ascending order) the Coral Bed, the Caliche Bed, the '*Waagenites*' Bed, the *Otoceras* Bed and the *Ophiceras* Bed (Jin et al. 1996). Of these, the Coral and Caliche Beds (beds 1–2 in Section A, Fig. 1, respectively) have been lithologically assigned to the Selong Formation, while the '*Waagenites*', *Otoceras* and *Ophiceras* Beds (beds 3–5 in Section A, Fig. 1, respectively) have been referred to the Kangshare Formation (Jin et al. 1996). One specimen described herein was collected from the '*Waagenites*' Bed. The conodont *Clarkina orchardi* Zone of latest Changhsingian age has been recorded from the same bed (Wang et al. 1989; Jin et al. 1996; Mei 1997). In this section the Permian–Triassic boundary is defined by the first occurrence of the conodont *Hindeodus parvus* at the base of the *Otoceras* Bed (Jin et al. 1996). '*Waagenites*' from the '*Waagenites*' Bed is distinct from the type species of *Waagenites*, and is referred to herein as *Tethyochonetes liaoi* sp. nov. Accordingly, the '*Waagenites*' Bed could now be renamed the *Tethyochonetes* Bed.

One specimen of *Tethyochonetes wongiania* (Chao) was collected from the Lungtan Formation in the Baizuyuan section of Nantong County of Chongqing City, southwest China (Section B, Fig. 1). The Lungtan Formation in this area is of Wuchiapingian age (Sheng & Jin 1994).

The Meishan section of the Changxing area, Zhejiang Province, eastern China, (Section C, Fig. 1), a prime candidate of the Global Stratotype Section and Point of the Permian–Triassic Boundary (Yin et al. 1996), has yielded several *Tethyochonetes* specimens from Bed 26 (the Black Clay Bed) of latest Changhsingian age.


Lazale
4800 m
Direasangba
Kairu-Ochen Lake
Tingri-Gyirong
A Selong Section
0 2 km
4800 m
4900 m
Highway
Selong
4700 m
1
0 25 km
Chongqing
Ba County
Yangtze River
B
Baizuyuan Section
Nantong
2
Meishan Section
C
Taihu Lake
Niutoushan
Changxing
D
Huangzhishan Section
Shian
0 10 20km
Huzhou
3
N
0 500 1000km
Beijing
A
B
C
D
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Tethyochonetes
4
LEGEND
1 2 3 4 5 6
7 8 9 11-12 10 11 12


A
Kangshare Fm.
Selong Fm.
Triassic
Permian
1 2 3 4 5
40 cm
0
B
Changhsing Fm.
Loping Fm.
Changhsingian
Wuchipingian
10m
0
C
Yinkeng Fm.
Changhsing Fm.
Triassic
Permian
24 25 26 27 28 29 35
0.15m
0
D
Yinkeng Fm.
Changhsing Fm.
Triassic
Permian
1 8 11 12 13 14 15 16
1m
0

The remaining material of *Tethyochonetes* described in this paper was obtained from Beds 11 and 12 of the Huangzhishan section (Section D, Fig. 1) of Huzhou City, Zhejiang Province, eastern China. Bed 12 is of earliest Triassic age because of the appearance of the associated bivalve species: *Pteria ussurica variabilis* Chen & Lan, *Towapteria scythica* (Writh) and *Eumorphotis* sp. The underlying Bed 11 is characterised by abundant brachiopods including *Neochonetes convexa* Liao, *Spinomarginifera kueichowensis* Huang, *Spinomarginifera alpha* Huang, *Haydenella chianensis* (Huang), *Crurithyris flabelliformis* Liao and *Araxathyris araxensis* Grunt, all common elements of the Changhsingian in South China (Liao 1979). The late Changhsingian conodont species *Clarkina changxingensis* Wang & Wang is also present in the underlying limestone beds (Zhang 1995), therefore constraining the age of Bed 11 to be most likely latest Changhsingian.

In addition, several specimens of true *Waagenites* from the Middle Permian of the Xiaoxinzai section (Locality 14, Fig. 1) in the Gengma area, western Yunnan are also figured herein for comparison with the new genus.

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION OF *TETHYOCHONETES* GEN. NOV.

Nine species of *Tethyochonetes* have been reported from different areas of China (Table 1). In addition, *Tethyochonetes soochowensis* (Chao) has been reported from the Changhsingian Yenduyet Formation of the Son La area of northwest Vietnam (Shi & Shen 1998). Species of *Tethyochonetes* range from Wuchiapingian to latest Changhsingian age and are palaeogeographically confined to the Cathaysian and Himalayan Provinces as defined by Shen et al. (1999).

SYSTEMATIC PALAEONTOLOGY

The supra-orderinal classification follows Williams et al. (1996). The classification of the Rugosochonetidae is after Archbold (1982). All morphological terms are in current use, as in Williams & Brunton (1997).

Phylum BRACHIOPODA Dumeril, 1806

Subphylum RHYNCHONELLIFORMEA Williams, Carlson, Brunton, Holmer & Popov, 1996

Class STROPHOMENATA Williams, Carlson, Brunton, Holmer & Popov, 1996

Order PRODUCTIDA Waagen, 1883

Suborder CHONETIDINA Muir-Wood, 1955

Superfamily CHONETOIDEA Bronn, 1862

Family RUGOSOCHONETIDAE Muir-Wood, 1962

Subfamily RUGOSOCHONETINAE Muir-Wood, 1962

Fig. 1. Fossil localities and geographic distribution of *Tethyochonetes* gen. nov. in China. ❶ Selong section, Nyalam County, southern Tibet. ❷ Baizhuyuan section, Nantong County, Chongqing City, southwest China. ❸ Meishan section, Changxing County, and Huangzhishan section, Huzhou City, Zhejiang Province, eastern China. ❹ Distribution of *Tethyochonetes* gen. nov. in China. 1. Longtan section, Nanjing City, Jiangsu Province, eastern China. 2. Miaojiao section, Suzhou City, Jiangsu Province, eastern China. 3. Meishan section, Changxing County, and Huangzhishan section, Huzhou City, Zhejiang Province, eastern China. 4. Huangzhishan section, Huzhou City, Zhejiang Province, eastern China. 5. Fushi section, Yongding County, Fujian Province, southeastern China. 6. Shuizutang section, Lianxian County, northern Guangdong Province, South China. 7. Loping coal mine section, Loping City, Jiangxi Province, South China. 8. Jiazhishan section, Anshuan City, Guizhou Province, southwestern China. 9. Huayinshan section, Hnayin City, Sichuan Province, southwestern China. 10. Shangsi section, Guangyuan City, Sichuan Province, southwestern China. 11. Yikebiqueisi and Delingha sections, Tianjun County, Qinghai Province, China. 12. Yinba section, Changdu City, eastern Tibet. 13. Selong section, Nyalam County, southern Tibet. 14. Locality of *Waagenites*: the Xiaoxinzai section, Gengma County, western Yunnan, China. Legend: 1, fossil horizon; 2, limestone; 3, argillaceous limestone; 4, marl; 5, black shale; 6, clay bed; 7, sandy mudstone; 8, siltstone; 9, sandstone; 10, bed number; 11, highway and railway; 12, city and county. Stratigraphic columns A–D provide details of lithological successions across several Permian–Triassic boundary sections in China. **A.** The Selong section (Fig. 1.1). Bed 1: the Coral Bed; Bed 2: the Caliche Bed; Bed 3: *Tethyochonetes* Bed (='*Waagenites*' Bed of Jin et al. 1996); Bed 4: *Otoceras* bed; Bed 5: *Ophiceras* Bed. **B.** The Baizhuyuan section (Fig. 1.2). **C.** The Meishan section (Fig. 1.3). **D.** The Huangzhishan section (Fig. 1.3). (Legends see above, the left numbers of Sections A, C and D represent beds.)

Species	Author	Formation and age	Locality see Fig. 1	Revision
Chonetes barusiensis (Davidson)	Hayaskaya 1922; Wang *et al.* 1964	? Late Permian	Loc. 8	*Tethyochonetes chaoi* gen. et sp. nov.
C. cf. *barusiensis* (Davidson)	Chao 1928	*Lyttonia* bed, Late Permian	Loc. 7	*T. chaoi* gen. et sp. nov.
Waagenites barusiensis (Davidson)	Jin & Liao 1974; Feng & Jiang 1978	Lungtan Fm., Wuchiapingian	Loc. 10	*T. chaoi* gen. et sp. nov.
	Zhang & Jin 1976	Selong Group, Late Permian	Loc. 13	*T. chaoi* gen. et sp. nov.
	Yang *et al.* 1977	Shuizutang Fm., Changhsingian	Loc. 6	*T. chaoi* gen. et sp. nov.
W. barusiensis (Davidson)	Xu 1987	Changhsing Fm., Changhsingian	Loc. 9	*T. chaoi* gen. et sp. nov.
	Zhan 1989	Talung Fm., Changhsingian	Loc. 10	*T. chaoi* gen. et sp. nov.
Tethyochonetes chaoi sp. nov.	This paper	Changhsing Fm., Changhsingian	Loc. 3, 4	*T. chaoi* gen. et sp. nov.
Waagenites barusiensis (Davidson)	Liao 1979, 1980a,b	Changhsing Fm., Changhsingian	Loc. 8	*Tethyochonetes liaoi* gen. et sp. nov.
	Zhao *et al.* 1981; Liao 1984	Talung and Yinkeng Fms., Changhsingian	Loc. 1, 3, 5	*T. liaoi* gen. et sp. nov.
	Zhan 1979,	Shuizutang Fm., Changhsingian	Loc. 6	*T. liaoi* gen. et sp. nov.
	Wang *et al.* 1982	Talung and Yinkeng Fms	Loc. 2, 3	*T. liaoi* gen. et sp. nov.
	Wang *et al.* 1989	Kanshare Fm. Changhsingian	Loc. 13	*T. liaoi* gen. et sp. nov.
Tethyochonetes liao sp. nov.	This paper	Changhsing and Kangshare Fms., Changhsingian	Loc. 3, 13	*T. liaoi* gen. et sp. nov.
Chonetes soochowensis Chao	Chao 1928	? Late Permian	Loc. 2	*Tethyochonetes soochowensis* (Chao)
	Huang 1932	? Late Permian	Loc. 8	*T. soochowensis* (Chao)
Waagenites soochowensis (Chao)	Yang *et al.* 1977; Zhan 1979	Shuizutang Fm., Changhsingian	Loc. 6	*T. soochowensis* (Chao)
	Liao 1979, 1980a, b; Feng & Jiang 1978	Changhsing Fm., Changhsingian	Loc. 13	*T. soochowensis* (Chao)
	Zhao *et al.* 1981; Liao 1984	Talung and Yinkeng Fms., Changhsingian	Loc. 3, 5	*T. soochowensis* (Chao)
	Wang *et al.* 1982	Changhsing Fm., Changhsingian	Loc. 3	*T. soochowensis* (Chao)
	Xu 1987	Changhsing Fm., Changhsingian	Loc. 9	*T. soochowensis* (Chao)
	Zhan 1989	Changhsing Fm., Changhsingian	Loc. 10	*T. soochowensis* (Chao)
	Zeng *et al.* 1995	Luntan Fm., Wuchiapingian	Loc. 10	*T. soochowensis* (Chao)
Chonetes wongiania Chao	Chao 1928	? Late Permian	Loc. 1	*Tethyochonetes wongiania* (Chao)
	Wang *et al.* 1964	? Late Permian	Loc. 8	*T. wongiania* (Chao)
Waagenites wongiania (Chao)	Yang *et al.* 1977; Zhan 1979	Shuizutang Fm., Changhsingian	Loc. 6	*T. wongiania* (Chao)
	Liao 1980a, b; Feng & Jiang 1978	Changhsing Fm., Changhsingian	Loc. 8	*T. wongiania* (Chao)
	Wang *et al.* 1982	Lungtan Fm., Wuchiapingian	Loc. 1	*T. wongiania* (Chao)
	Xu 1987	Changhsing Fm., Changhsingian	Loc. 9	*T. wongiania* (Chao)
	Zhan 1989	Changhsing Fm., Changhsingian	Loc. 10	*T. wongiania* (Chao)
	Zeng *et al.* 1995	Luntan Fm., Wuchiapingian	Loc. 10	*T. wongiania* (Chao)
Tethyochonetes wongiania (Chao)	This paper	Lungtan Fms., Wuchiapingian	Loc. 9	*T. wongiania* (Chao)
W. soochowensis quadrata Zhan	Zhan 1979	Shuizutang Fm., Changhsingian	Loc. 6	*Tethyochonetes quadrata* (Zhan)
Tethyochonetes quadrata (Zhan)	This paper	Changhsing Fm., Changhsingian	Loc. 4	*T. quadrata* (Zhan)
Waagenites pigmaea Liao	Liao 1979, 1980a, b	Changhsing Fm., Changhsingian	Loc. 8	*Tethyochonetes pigmaea* (Liao)
	Zhao *et al.* 1981; Liao 1987	Talung and Yinkeng Fms., Changhsingian	Loc. 1, 2, 3, 5	*T. pigmaea* (Liao)
	Wang *et al.* 1982	Changhsing Fm., Changhsingian	Loc. 3	*T. pigmaea* (Liao)
Waagenites guizhouaensis Liao	Liao 1980a	Changhsing Fm., Changhsingian	Loc. 8	*Tethyochonetes guizhouensis* (Liao)
Waagenites longtanensis Liao	Liao 1984	Talung Fm., Changhsingian	Loc. 1	*Tethyochonetes longtanensis* (Liao)
Tethyochonetes longtanensis (Liao)	This paper	Changhsing Fm., Changhsingian	Loc. 4	*T. longtanensis* (Liao)
Waagenites convexa Fan	Yang *et al.* 1962	? Late Permian	Loc. 11	*Tethyochonetes convexa* (Fan)
	Jin & Sun 1981; Jin 1985	Yinba & Toha Fms., Late Permian	Loc. 12	*T. convexa* (Fan)

Table 1. Geographic and stratigraphic distributions of species of *Tethyochonetes* gen. nov.

Discussion. Archbold (1982) formally grouped the rugosochonetid genera into six subfamilies. Of these, the Rugosochonetinae was restricted to include only the externally capillated to costated genera. In addition to external ornament, the subfamily can also be distinguished from other rugosochonetids in embracing a feebly to strongly developed ventral median sulcus, usually low-angle hinge spines, and well-developed brachial ridges in the dorsal valve.

Genus **Tethyochonetes** gen. nov.

Etymology. Latin. *Tethy-* Tethys, referring to the Sister and Consort of Oceanus (the god of the ocean in Greek mythology) (the first English publication, Suess 1893: 183). The genus is limited to the Lopingian of the Tethyan region of the Palaeoequatorial Realm.

Type species. *Waagenites soochowensis quadrata* Zhan 1979.

Diagnosis. Small and transversely rectangular Rugosochonetidae, profile strongly concavo-convex; cardinal extremities varying from acute to slightly semi-elliptical; ears smooth, broad, flattened or slightly swollen. Ventral sulcus varying from deep, broad and distinct to shallow, narrow and indistinct; sulcal bounding flanks distinct to depressed. Dorsal fold slightly raised to flattened. External ornament with robust and rounded costae, sometimes bifurcating. Ventral median septum thin and high, extending anteriorly for half valve length. Cardinal process rounded and blunt, bilobed internally, trilobed externally; dorsal median septum stout, raised at its middle to anterior part, originating anterior to alveolus, continuing forward for half valve length; lateral septa stout, short and distinct; brachial scars strongly swollen and semi-circular in shape.

Other included species. As shown on Table 1.

Discussion of specific variation. Of nine species currently assigned to *Tethyochonetes* gen. nov., the older species such as *T. wongianus* (Chao), flourishing at the Wuchiapingian, usually embrace larger size and extremely coarse costae (see below). In comparison, the younger species often are much smaller and have finer ribs. In particular, two younger species, *T.? liaoi* sp. nov. and *T. longtanensis* (Liao), both from the latest Changhsingian, are significantly smaller, usually less 10 mm in width, and possess finer ribs than others (see below). However, all of them embrace highly convex ventral valve, and more importantly, share the same internal characteristics. Accordingly, they are tentatively referred to the new genus.

Comparison. Species of *Waagenites* Paeckelmann, 1930 invariably possess subquadrate and strongly concavo-convex shells, with large inflated ears and coarse costae (Figs 2A–C, 3Q, T). As discussed by Fang (1983) and Archbold (1988), the ventral interior is characterised by strong teeth, a short but distinctive median septum and a median ridge. The median ridge commences at the anterior of the median septum and is high anteriorly because of the presence of taleolae (Figs 2D, 3F–G). The cardinal process is trilobate externally with a deep alveolus; the myophore faces ventrally through the open delthyrium (Fig. 3J–K, R–S). A thin, high median septum arises anterior to the alveolus and is highest at its middle-anterior part; the lateral septa are short, strong and distinct; the brachial scars are strongly convex and semi-circular in shape (Figs 2E, 3L).

Morphologically, *Waagenites* is closest to *Tethyochonetes* in both external and internal features. However, the new genus is distinguished by the possession of distinct but finer costae, less strongly concavo-convex shells and less distinct sulcus and fold. In addition, *Waagenites* has a prominent median ridge and a rather short ventral median septum, often shorter than one fifth of the valve length (Figs 2D, 3F–G). In contrast, *Tethyochonetes* gen. nov. bears a long ventral median septum, usually longer than half of the valve length (see Yang et al. 1962: 48, pl. 14, fig. 14). The dorsal interior of *Waagenites* is characterised by a broad, deep alveolus, and a thin, high, blade-like median septum (Fig. 2E), whereas *Tethyochonetes* has a shallow alveolus, and a stout median septum and lateral septa (Fig. 2F).

The younger species of *Tethyochonetes* somewhat resemble *Neochonetes* in terms of fine ribs, however, *Neochonetes* is easily separated from the new genus by its paucicostellae, paucicostellate ears and pair of well-developed vascular trunks in the ventral valve.

Tethyochonetes shares features with other genera notably *Fusichonetes* Liao (in Zhao et al. 1981), *Fanichonetes* Xu & Grant (1994), *Waterhouseiella* Archbold (1983) and *Rugaria* Cooper & Grant (1969). A comparison of these genera with *Tethyochonetes* is provided in Table 2. Diagnostic features of *Tethyochonetes* are a relatively long ventral median septum, a strong, long dorsal median septum, arising anteriorly of the alveolus, and brachial scars that are strongly convex and semicircular.

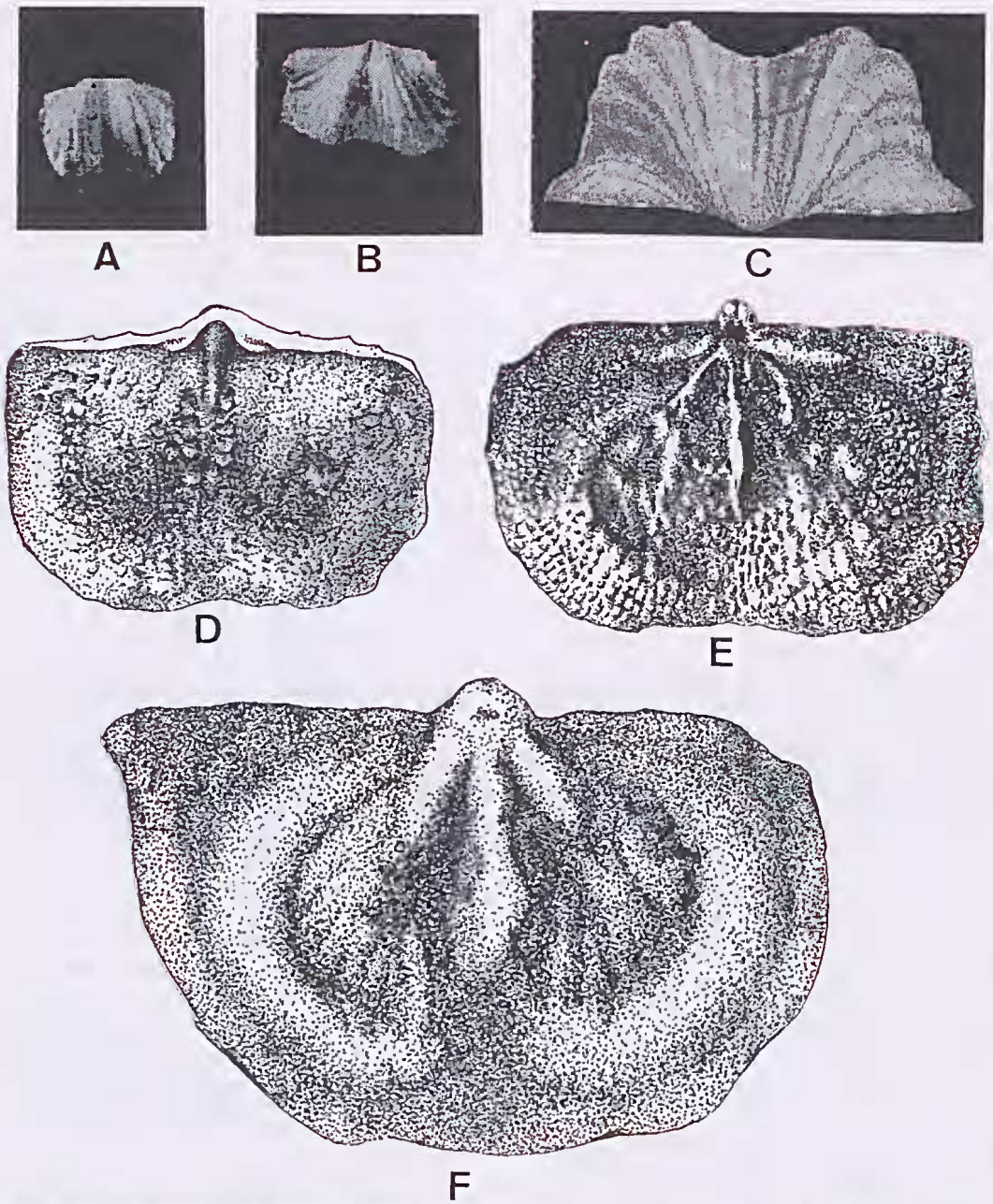


Fig. 2. External features of topotype specimen and internal features of *Waagenites* Paeckelmann, 1930 and *Tethyochonetes* gen. nov. A–C, *Waagenites grandicosta* (Waagen), type species of the genus. A–B, two ventral valves from the Chhidru Formation of Punjab, Salt Range, Pakistan (after Muir-Wood 1965: H433, fig. 288, 3b, e), ×1.5, ×2, respectively. C, posterior view of a ventral valve from the Chhidru Formation of the Salt Range, Pakistan (after Waagen 1884: pl. 61, fig. 7a), ×4. D–E, *Waagenites yunnanensis* Fang. D, a ventral valve interior (drawing based on specimen NMV P1456843; see also Fig. 3N, P), showing a short median septum, ×5. E, a dorsal valve interior (figure based on specimen 81111 illustrated by Fang [1983: 96, pl. 2, fig. 3] from the Middle Permian of the Xiaoxinzai section [Locality 14, Fig. 1.4]), ×5. F, the dorsal internal features of *Tethyochonetes quadrata* (Zhan) (figure based on specimen K-0066 [Zhan 1979: 70–71, pl. 4, fig. 16], housed in the Chinese Academy of Geological Sciences, Beijing), ×6.

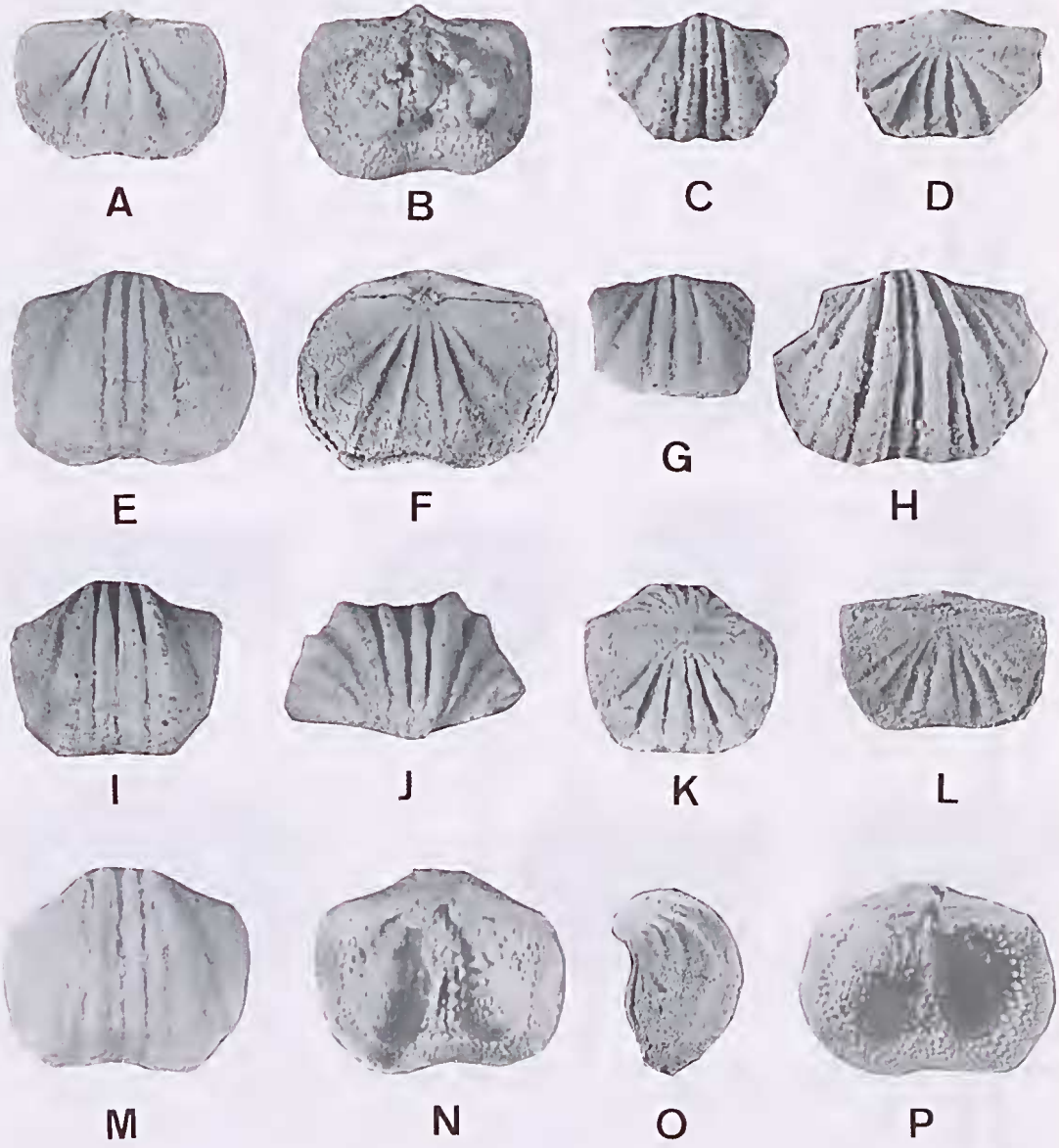


Fig. 3. Waagenites yunnanensis Fang. A–B, NMV P149270, a dorsal valve exterior and interior, ×3.5, ×4. C–D, NMV P149271, a complete specimen in ventral and dorsal views, ×3.5. E–F, NMV P1456843, a complete specimen in ventral and dorsal views, ×4. G–H, NMV P149272–273, two specimens in ventral views, ×3.5. I–K, NMV P149274, a complete speeimen in ventral, posterior and dorsal views, ×3.5. L, NMV P149275, a specimen in dorsal view, ×3.5. M–N, NMV P1456848, a ventral valve exterior and interior, ×4. O–P, NMV P149276, a ventral valve in lateral and interior views, ×4. All from the Middle Permian of the Xiaoxinzai section (Locality 14, Fig. 1.4).

	Characteristic \ Genera	*Waagenites* Paeckelmann	*Tethyochonetes* gen. nov.	*Fusichonetes* Liao	*Fanichonetes* Xu & Grant	*Waterhouseiella* Archbold	*Rugaria* Cooper & Grant
Exterior	Hinge spine	4-5 pair, extending latero-posteriorly	2-4 pair, extending latero-posteriorly	3-4 pair, extending latero-posteriorly	6-8 pair, inclined toward midline	7-8 pair, extending latero-posteriorly	5-6 pair, extending latero-posteriorly
	HW/SW	1 or <1	1	1	1.0-1.2	1	0.9-1.1
	SW/SL	1.4-1.7	1.2-1.9	3.2	1.2-1.4	1.4-1.6	1.3-1.5
	SW/ST	2.0-2.5	1.5-3.5	?	?	3.1-3.6	5.1-5.3
	Ears	moderate size, inflated	large, flat	large, flat	large, flat	large, flat	small or undeveloped
	Costation pattern: density (per 5 mm at midvalve)	2-3	8-10	12	11-13	6-7	16
	Costation pattern: interspace	deep, wide & angular	moderately deep, wide and rounded	deep, angular	narrow & shallow	deep, rounded	moderately deep, rounded
	Costation pattern: subdivision	bifurcation	bifurcation	simple	bifurcation	branching or intercalation	bifurcation
Interior	Ventral valve: median septum	short,	long, up to midlength	?	short	high, thin, long up to midlength	short
	Ventral valve: vascular trunks	distinct	no	no	no	variably developed	no
	Dorsal valve: cardinal process	small, trilobate	broad & strong, trilobate	?	bifid	low	broad
	Dorsal valve: median septum	blade like, up to midlength arising anteriorly	strong, long arising anteriorly	?	?	develop at midvalve	excavated anteriorly
	Dorsal valve: lateral septa	strong and short	strong and short	?	?	long	undeveloped
	Dorsal valve: brachial scars	strongly convex, semicircular	strongly convex, semicircular	?	?	no	no

Table 2. Comparison of *Tethyochonetes* gen. nov. with allied genera. HW/SW: the ratio of hinge width and greatest width of shell; SW/SL: the ratio of valve width and valve length; SW/ST: the ratio of valve width and thickness. Question marks indicate information that was not provided by the original authors when the genera were proposed.

Discussion. Most of the costate, rugosochonetid specimens from the Late Permian of China, considered previously to belong to *Waagenites*, possess the diagnostic features of the new genus and are different from true *Waagenites* as characterised above. We therefore refer these Chinese species to *Tethyochonetes* gen. nov.

Tethyochonetes quadrata (Zhan 1979)

(Fig. 4A–D, G)

Waagenites soochowensis quadrata Zhan 1979: 70, pl. 4, figs 16–19.

Holotype. Designated by Zhan (1979: 70), Specimen K-0063 from the Late Permian Shuizutang Formation of

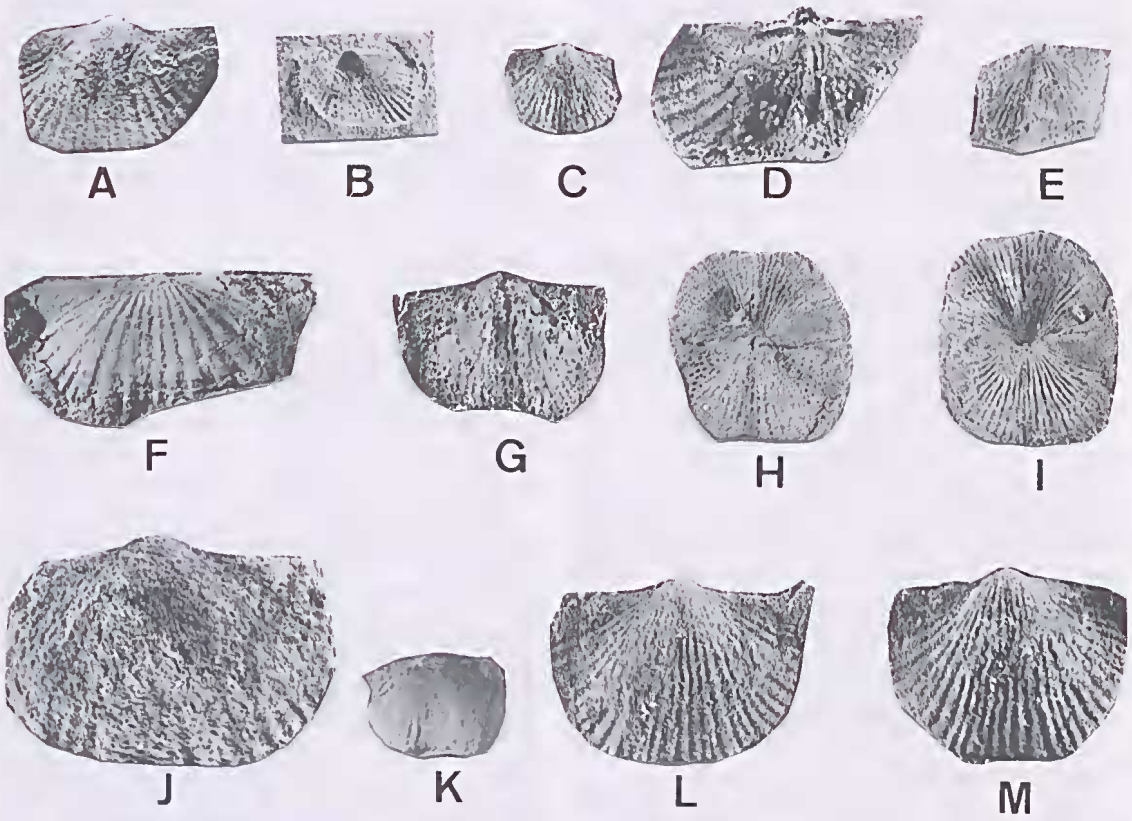


Fig. 4. A–D, G, *Tethyochonetes quadrata* Zhan. All specimens from the Changhsingian Changhsing Formation of the Huangzhishan section (Locality 4, Fig. 1.4), ×3. A, a ventral valve (NIGP 130460), ×3. B–C, views of an external mould of a ventral valve and a shelly ventral valve (NIGP 130462), ×1.5. D, a dorsal internal mould (NIGP 130459), ×3. G, a ventral internal mould (NIGP 130461), ×3. E, H–I, *Tethyochonetes? liaoi* sp. nov. E, a ventral external mould (NMV P149277), ×2, from the Kangshare Formation of the Selong section (Locality 13, Fig. 1.4). H–I, two ventral valves and external moulds (NIGP 130464–130465), ×3, from the Changhsingian Changhsing Formation of the Huangzhishan section (Locality 4, Fig. 1.4). F, *Tethyochonetes wongiania* (Chao). A dorsal external mould (NMV P149278), ×2, from the Wuchiapingian Lungtan Formation of the Baizuyuan section (Locality 9, Fig. 1.4). J–K, *Tethyochonetes chaoi* sp. nov. All specimens from the black shale (Bed 26 in Section C, Fig. 1) of the latest Changhsingian Yinkeng Formation of the Meishan section (Locality 3, Fig. 1.4). J, a ventral valve (NIGP HZ 130475), ×5. K, a ventral valve (NMV P1456860), ×2. L–M, *Tethyochonetes longtanensis* (Liao). Two ventral valves (NIGP 130471–130472), ×3, from the Changhsingian Changhsing Formation of the Huangzhishan section (Locality 4, Fig. 1.4).

Lian Xian, Northern Guangdong, figured by Zhan (1979: pl. 4, fig. 17a–b), and housed in the Chinese Academy of Geological Sciences, Beijing, China.

Material. Figured specimens include two ventral valves, a ventral internal mould, a ventral external mould, and a dorsal internal mould (NIGP 130459–130462).

Measurements (in mm)

Specimens	Valve length	Hingeline width	Midvalve width	Thickness
NIGP 130459	3.73	7.02	7.05	2.03 ▲
NIGP 130460	4.72	7.75	7.55	2.68 ♥
NIGP 130461	5.61	8.48	7.99	2.84 ♥
NIGP 130462	3.89	4.41	4.22	2.95 ♥

♥ only ventral valve; ▲ only dorsal valve (the same legend hereafter)

Diagnosis. Small and subquadrate *Tethyochonetes*; ventral umbo rounded; median sulcus variously developed; costae moderately coarse. Shell internally pustulose.

Description. Transversely quadrate to rectangular in outline; hingeline straight and equal to shell width; cardinal extremities varying from acute to slightly semi-elliptical; ears smooth, large, flattened or slightly swollen, distinct; separated from body of shell by grooves.

Ventral valve strongly to moderately convex; beak broadly, evenly convex and strongly incurved, overhanging hingeline; interarea narrowly triangle-shaped, about 5 mm in width; umbo broadly rounded, convex, moderately steeply sloping to flanks; median sulcus varying from deep, broad, and distinct, to shallow, narrow and indistinct, originating anterior to beak and extending anteriorly with increasing width; flanks bounding sulcus vary from distinctly to weakly developed.

Dorsal valve deeply concave, median fold slightly raised to flattened, originating at beak, extending to anterior margin.

External surface ornamented by distinct and rounded costae, occasionally increasing in number near anterior margin by bifurcation; about 25 costae on external surface and 6 costae per 3 mm near anterior margin; costae in median sulcus slender and finer than those on other parts of shell. Posterior margin usually marked by about 2–4 oblique cardinal spines on each side.

Delthyrium distinct; hinge teeth well-developed; ventral median septum thin and high, originating under delthyrium and extending anteriorly to about half valve length. Cardinal process rounded and blunt, alveolus shallow; socket ridges parallel to hinge margin; dorsal median septum moderately high and strong, originating at anterior of alveolus and continuing forward for half of valve length, higher at middle-anterior part; lateral septa short, strong and distinct; brachial scars strong, swollen, and semi-circular in shape (Fig. 2F). Shell internal surface covered by abundant pustoles in radial rows.

Discussion. This species was first proposed as the subspecies *Waagenites soochowensis quadrata* based on specimens from the Late Permian Shuizutang Formation of Lian Xian, North Guangdong (Locality 6, Fig. 1). Compared with the holotype of *Chonetes soochowensis* Chao (1928: 31, pl. 1, figs 14–16), the Guangdong specimens are distinguished by their rectangular outline, more convex ventral valve, larger number of costae, and a more strongly elevated dorsal median septum. *Chonetes soochowensis* is also highly transverse, with a width/length ratio close to 2, more projecting cardinal extremities, and 16–18 costae on both valves. Therefore, Zhan's subspecies is regarded by us as a distinct species and assigned to *Tethyochonetes*.

Tethyochonetes quadrata has a similar dorsal median septum to that of *Waagenites yunnanensis* Fang (1983), being higher at its anterior-middle part, but the median septum of *T. quadrata* is more strongly developed and robust. *T. quadrata* possesses denser and finer costae, a longer ventral median septum, stronger lateral septa, and more strongly convex brachial scars than *W. yunnanensis*.

Tethyochonetes quadrata differs from *T.? liaoi* sp. nov. by its quadrate outline, moderately convex ventral valve and shallower median sulcus. The latter species has relatively larger, more inflated ears, and greater number of costae.

Tethyochonetes convexa (Fan in Yang et al. 1962: 48, pl. 14, figs 11–14) from the Late Permian of the Tibet–Qinghai region, western China (Jin & Sun 1981: 131, pl. 1, fig. 6; Jin 1985: pl. 5, figs 4–5; pl. 7, fig. 12) may be distinguished from the present species by its narrower and deeper median sulcus, broader and more distinctive ventral interarea, and a longer ventral median septum.

Tethyochonetes guizhouensis (Liao 1980) [= *Waagenites guizhouensis* Liao 1980b: 258, pl. 5, figs 5–7; Zhan 1989: 25, fig. 5; = *Sulcirugaria guizhouensis* (Liao), Waterhouse 1983: 117] is distinct in being more transverse, twice as wide as long, and having broader ears, and unbranching costae.

Age and locality. Changhsingian; Huangzhishan section, Huzhou City, Zhejiang Province, eastern China.

Tethyochonetes chaoi sp. nov.

(Fig. 4J, K)

Etymology. Named for the late Dr Yah-Tseng Chao, a pioneer worker on the Permian brachiopods of China.

Chonetes barusiensis (Davidson), Hayaskaya 1922: 100, pl. 5, figs 7–10.—Wang et al. 1964: 240–241, pl. 27, figs 27, 33.
Chonetes cf. *barusiensis* (Davidson), Chao 1928: 30, pl. 1, fig. 18.
Waagenites barusiensis (Davidson), Jin & Liao 1974: 311, pl. 164, fig. 8.—Yang et al. 1977: 332, pl. 135, fig. 4.—Feng & Jiang 1978: 244, pl. 88, fig. 6.—Xu 1987: pl. 8, figs 17, 18; pl. 9, figs 7, 8, 21.—Zhan 1989: pl. 25, fig. 9.
Waagenites cf. *barusiensis* (Davidson), Zhang & Jin 1976: 65, pl. 1, fig. 7.

Holotype. Specimen (NIGP 22489) from the Lungtan Formation of the Late Permian of the Wenxing area, Chongqing City, selected herein, figured by Jin & Liao (1974: 311, pl. 164, fig. 8), and housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Material. Two ventral valves (NIGP 130475 and NMV P1456860) are illustrated.

Measurements (in mm)

Specimens	Valve length	Hingeline width	Midvalve width	Thickness
NMV P1456860	5.58	6.98	6.96	2.30 ♥
NIGP 130475	5.61	7.31	7.31	2.45 ♥

Diagnosis. Small and trapezoidal *Tethyochonetes*, with broad, deep ventral median suleus, seulptured with robust, simple, unbranching costae.

Description. Hingeline straight and equal to shell width; ears broad, smooth, flat or slightly inflated and projeeting laterally, separated by a trough or shallow coneavity from lateral flanks of ventral valve.

Ventral valve more or less strongly convex; beak arched, and extending slightly beyond hingeline; umbonal region broad and convex, flanked by steep lateral slopes; distinet median sulcus originating at beak, extending anteriorly and greatly increasing in width and depth, bounded by pronounced flanks. Dorsal valve deeply coneave; median fold indistinet.

External surfaees ornamented by 16 robust eostae with rounded erests; eostae originating at beak, simple and unbranching.

Internal features are normal for genus.

Discussion. *Waagenites barusiensis* (Davidson 1866) was based on a Himalayan speeimen. The original deseription and illustration provided by Davidson (1866: 42, pl. 2, fig. 7) indieates that the species should be referred to *Waagenites* Paeckelmann (1930) although its incomplete preservation hinders a full diagnosis (Waterhouse & Piyasin 1970: 117).

Many Chinese Late Permian ehonetid speei-mens have been compared or identified with *W. barusiensis*, but differ from the type material of true *W. barusiensis* in possessing relatively less strongly coneavo-convex shell, a narrower and shallower median suleus and a differing number of eostae. The large morphologieal variations of these various Chinese reports allows us to propose two new speeies, *T. chaoi* sp. nov. and *T.? liaoi* sp. nov.

Tethyochonetes soochowensis (Chao 1928), a eommon speeies in the Late Permian in Asia (Table 1), may be distinguished from the present species by its very transverse outline, shell width double shell length, flat and postero-laterally projeeting ears and aeute eardinal extremities.

Age and locality. Changhsingian; Meishan sceetion, Changxing, Zhejiang Province, eastern China.

Tethyochonetes? liaoi sp. nov.

(Fig. 4E, H–I)

Etymology. Named for Professor Liao Zhuoting of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Waagenites barusiensis (Davidson), Zhan 1979: 71, pl. 4, figs 15, 20.—Liao 1979: pl. 1, figs 16, 17.—Liao 1980a: pl. 5, figs 24–26.—Liao 1980b: 292, pl. 2, fig. 14.—Zhao et al. 1981: pl. 8, figs 9–12.—Wang et al. 1982: 197, pl. 96, figs 13, 30.—Liao 1984: pl. 1, fig. 12.—Wang et al. 1989: pl. 1, fig. 6.

Holotype. Designated herein, Specimen AJ12/43567 from the Lungtan Formation of Jiazhishan section of Anshuan City, Guizhou, figured by Liao (1980a: pl. 5, fig. 26) and housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Material. Three figured ventral valves (NMV P1456859, NIGP 130464 and NIGP 130465).

Measurements (in mm)

Specimens	Valve length	Hingeline width	Midvalve width	Thickness
NMV P1456859	6.13	9.48	8.37	3.12 ♥
NIGP 130464	3.85	7.21	6.33	3.80 ♥
NIGP 130465	3.94	7.56	6.87	3.91 ♥

Diagnosis. Small to medium sized *Tethyochonetes*, with trapezoidal outline; ears inflated; median sulcus narrow, deep; external ribs fine, occasionally bifurcate.

Description. Widest at straight hingeline; ears broad, smooth and inflated, bounded by shallow troughs from body of shell.

Ventral valve less strongly convex; beak strongly incurved and extending slightly beyond hingeline; umbo moderately convex; median sulcus originating at beak as a groove, greatly increasing width and depth anteriorly, bounded by distinct flanks. Dorsal valve deeply concave; median fold distinct, commencing at beak.

External ornamentation consisting of costellae with rounded crests, originating at beak, occasionally bifurcate anteriorly; about 5 costae per 10 mm near anterior margin.

Ventral interior with pair of strong teeth; median septum thin, long. Cardinal process strong, trilobed externally; alveolus circular and deep; dorsal median septum strong, raised at anterior; brachial scars distinct.

Discussion. *Tethyochonetes liaoi* sp. nov. is proposed for specimens referred by Zhan (1979), Liao (1979, 1980a, 1980b, 1984), Zhao et al. (1981), Wang et al. (1982), and Wang et al. (1989) to *Waagenites barnsiensis* (Davidson) (see above synonymy list). The new species is distinct from other members of the genus by its relatively narrower, deeper median sulcus, and significantly finer ribs. As a result, the present new species may be separated generically. However, strongly convex ventral valve, broad and smooth ears, and comparable internal structure allow the present tentative generic assignment.

The most allied species to the new species is *T. chaoi* sp. nov., both having a trapezoidal outline, broad, inflated ears, and deep, distinct ventral median sulcus, however, relatively finer, occasionally bifurcate capillae and slightly more strongly inflated ears distinguish the new species from the latter.

Tethyochonetes pigmaea (Liao 1979) [= *Fusichonetes pigmaea* Liao 1979: pl. 1, fig. 14; 1980b: pl. 1, figs 5–6; Zhao et al. 1981: pl. 8, fig. 7; Wang et al. 1982: 200, pl. 96, figs 8–9; = *Plicochonetes pigmaea* (Liao), Liao 1980a: 257, pl. 4, figs 4–6; = *Waagenites pigmaea* (Liao), Liao 1984: 279, pl. 1, fig. 7; 1987: 100, pl. 3, fig. 24] is distinguished by being much smaller and having smaller, less inflated ears, simple, unbranching, smaller number of costae, and a less well-developed ventral median septum.

Tethyochonetes convexa (Fan in Yang et al. 1962) is separated by means of its broader ventral umbonal region and prominent teeth. *T. convexa* is also lamellose near its anterior margins.

Age and localities. Changhsingian; Selong section, Nyalam County, southern Tibet and Huangzhishan section of Huzhou City, Zhejiang Province, eastern China.

Tethyochonetes longtanensis (Liao 1984)

(Fig. 4L, M)

Waagenites longtanensis Liao 1984: 279, pl. 1, figs 8–9.

Holotype. Designated by Liao (1984: 279, pl. 1, fig. 9), Specimen 71125 from the Talung Formation of the Longtan section, Nanjing, Jiangsu Province, housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Material. Two ventral valves are figured (NIGP 130471–130472).

Measurements (in mm)

Specimens	Valve length	Hingeline width	Midvalve width	Thickness
NIGP 130471	7.45	10.71	10.07	3.61 ♥
NIGP 130472	7.33	10.16	9.85	3.59 ♥

Diagnosis. Medium sized *Tethyochonetes*, with transversely quadrate outline, highly convex ventral umbo, and flat ears.

Description. Widest at hingeline, cardinal extremities acute; ears large, smooth or ornamented by weak costae, forming generally an acute extension at cardinal extremities and demarcated shell flanks by pronounced concavity.

Ventral valve strongly convex; greatest convexity at umbo; beak strongly arched, slightly extending beyond hingeline; umbonal region high and narrow, triangular-shaped; median sulcus well-developed, deep but narrow. Dorsal valve slightly concave; beak indistinct; median fold distinct.

External costae dense, with narrower costal interspaces, commencing at beaks, about 3–4 per 2 mm at anterior margin; posterior margin marked by 3–4 pairs of spines on each side, projecting laterally.

Ventral median septum low but long. Cardinal process low; sockets open and distinct; median septum thin and long, originating from anterior of alveolus and extending forward to midvalve, arising slightly at its anterior end; lateral septa strong and short.

Discussion. The most allied species is *T. guizhouensis* (Liao), which possesses unbranching, coarse costae, but *T. guizhouensis* is relatively more transverse, with shell width double the shell length, and embraces more laterally projecting cardinal extremities.

The present species resembles *T. quadrata* (Zhan) in embracing a subquadrate outline, closely spaced costae, but has a relatively shallower ventral median sulcus, a more highly convex ventral umbo, which have steeper slopes to flanks, and a thinner median septum in the dorsal interior.

T. chaoi sp. nov. is distinguishable from the present species by the possession of a broader, less strongly convex ventral umbonal region, a broader median sulcus, and relatively coarser, a smaller number of costae.

The present species is differentiated from *T.? liaoi* sp. nov. by possessing a narrower and more strongly convex ventral umbonal region, juvenile stages, and a narrower ventral median sulcus.

Age and locality. Changhsingian; Huangzhishan section, Huzhou City, Zhejiang Province, eastern China.

Tethyochonetes wongiania (Chao 1928)

(Fig. 4F)

Chonetes wongiania Chao 1928: 28, pl. 1, fig. 17.—Wang et al. 1964: 242, pl. 37, fig. 28.

Waagenites wongiania (Chao), Yang et al. 1977: 332, pl. 136, fig. 8.—Zhan 1979: 72, pl. 11, fig. 7.—Liao 1980a: pl. 5, fig. 4.—Liao 1980b: pl. 1, fig. 2; pl. 2, fig. 7.—Feng & Jiang 1978: 243, pl. 88, fig. 5.—Wang et al. 1982: 198, pl. 91, figs 1–2; pl. 95, fig. 6.—Xu 1987: 220, pl. 9, figs 1, 2, 5–6, 10–12.—Zhan 1989: pl. 25, fig. 10.—Zeng et al. 1995: pl. 3, fig. 18.

Holotype. Designated by Chao (1928: 31), Specimen Cat. No. 539 from the Luntan Formation of Miaojiao section, Suzhou City, Jiangsu Province, figured by Chao (1928: pl. 1, fig. 14), housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Material. Figured specimen, a ventral valve (NMV P1456861).

Measurements. Length 8.17 mm, width 17.04 mm, thickness 3.03 mm.

Diagnosis. Medium to large *Tethyochonetes*, with subtrapezoidal outline; ears rather broad; costae robust.

Description. Hingeline straight and equal maximum shell width; cardinal extremities acute; ears large and flat, demarcated from remainder of shell by a pronounced concavity.

Ventral valve strongly convex; beak strongly incurved, slightly extending beyond hingeline; umbonal region high, flanked by steep umbonal slopes; median sulcus well developed, broad and deep. Dorsal valve slightly concave; beak indistinct; median fold weakly developed.

External costae with relatively broader costal interspaces, simple throughout and unbranching, originating at beaks, becoming coarser near anterior margin, costae within median sulcus slender numbering about 16–20.

Internal features are similar to those of *T. quadrata* (Zhan).

Discussion. The present species bears relatively most robust costae than any other members of the genus, and thus, apparently resembles species of *Waagenites*. However, apart from the differences of internal structures documented in the above generic comparison, *T. wongiania* has a less highly convex ventral valve, relatively broader ears and slightly greater number of costae, which usually have more flattened crests.

T. wongiania is remarkably similar to *T. soochowensis* (Chao) in outline, external ornament and dorsal internal features, but differs from the latter in possessing a broader and deeper ventral median sulcus, and simple, unbranching, less closely spaced costae.

T. guizhouensis (Liao) is also comparable with the present species in many details, but can be differentiated by being more transverse, and having slightly finer, greater number of costae and a less developed ventral sulcus.

Horizon and locality. Wuchiapingian; Baizuyuan section, Nantong County, Chongqing City, southwestern China.

ACKNOWLEDGEMENTS

We particularly wish to thank Ms Danjie Chen for her drawing the figures. Provision by Dr Fang Renseng of *Waagenites* specimens from western Yunnan is also greatly acknowledged. This study was carried out when the senior author was a recipient of an Overseas Postgraduate Research Scholarship tenurable at Deakin University, a Deakin University Postgraduate Research Award, and a Research Award (1998) of the Royal Society of Victoria. The study is supported by the Australian Research Council.

REFERENCES

ARCHBOLD, N. W., 1982. Classification and evolution of the Brachiopod Family Rugosochonetidae Muir-Wood 1962. *Proceedings of the Royal Society of Victoria* 94: 1–9.

ARCHBOLD, N. W., 1983. Permian marine invertebrate provinces of the Gondwanan Realm. *Alcheringa* 7: 59–73.

CHAO, Y. T., 1928. Productidae of China, II: Chonetinae, Productinae and Richthofeniinae. *Geological Survey of China, Palaeontologia Sinica, series B* 5(3): 1–103, 6 pls.

COOPER, G. A. & GRANT, R. E., 1969. New Permian brachiopods from west Texas. *Smithsonian Contributions to Paleobiology* 1: 1–20, 5 pls.

DAVIDSON, T., 1866. Notes on the Carboniferous Brachiopoda, collected by Captain Godwin-Austen in the Valley of Kashmere. *Quarterly Journal of the Geological Society of London* 22(1): 39–45, 1 pl.

FANG, R. S., 1983. The Early Permian Brachiopoda from Xiaoxinzhai of Gengma Yunnan and its geological significance. *Contributions to the Geology of the Qinghai-Xizang (Tibet) Plateau* 11: 93–119, 7 pls. (In Chinese.)

FENG, R. L. & JIANG, Z. L., 1978. Brachiopoda. In *Palaeontological Atlas of Southwestern China, Guizhou Province* 2: 231–304, pls 85–108. Geological Publishing House, Beijing. (In Chinese.)

GRANT, R. E., 1976. Permian brachiopods from southern Thailand. *Journal of Paleontology* 50(3), *Paleontological Society, Memoir* 9: 1–269, 71 pls.

HAYASKAYA, I., 1922. Paleozoic brachiopods from Japan, Korea and China. Pt 1. Middle and Southern China. *Tohoku Imperial University Science Reports, Series 2 (Geology)* 6(1): 1–137, 5 pls.

HUANG, T. K., 1932. Late Permian Brachiopods of Southwestern China. Pt 2. *Geological Survey of China, Palaeontologia Sinica, Series B* 9(1): 1–138, 9 pls.

JIN, Y. G., 1985. Permian Brachiopoda and palaeogeography of the Qinghai-Xizang (Tibet) Plateau. *Palaeontologia Cathayana* 2: 19–71, 8 pls.

JIN, Y. G. & LIAO, Z. T., 1974. Carboniferous and Permian brachiopods. In *A Handbook of the Stratigraphy and Palaeontology in Southwest China*, Nanjing Institute of Palaeontology and Geology, Academia Sinica. Science Press, Beijing, 275–282, pls 142–147; 308–313, pls 162–165. (In Chinese.)

JIN, Y. G., SHEN, S. Z., ZHU, Z. L., MEI, S. L. & WANG, W., 1996. The Selong section, candidate of the Global Stratotype Section and Point of the Permian–Triassic Boundary. In *The Palaeozoic–Mesozoic Boundary Candidates of Global Stratotype Section and Point of the Permian–Triassic Boundary*, H. F. Yin, ed., China University of Geosciences Press, Wuhan, China, 127–137, pls V.1–3.

JIN, Y. G. & SUN, D. L., 1981. Paleozoic brachiopods from Xizang. In *Palaeontology of Xizang Book III. The Series of the Scientific Expedition to the Qinghai-Xizang Plateau*, Science Press, Beijing, 127–275, 12 pls. (In Chinese.)

LIAO, Z. T., 1979. Brachiopod assemblage zones of Changhsingian Stage and Brachiopoda of the mixed fauna in South China. *Journal of Stratigraphy* 3(3): 200–213, 1 pl. (In Chinese.)

LIAO, Z. T., 1980a. Upper Permian brachiopods from Western Guizhou. In *Stratigraphy and Palaeontology of Upper Permian Coal-bearing Formation in Western Guizhou and Eastern Yunnan*, Nanjing Institute of Geology and Palaeontology, Academia Sinica, eds, Science Press, Beijing, 241–277, 9 pls. (In Chinese.)

LIAO, Z. T., 1980b. Brachiopod assemblages from the Upper Permian and Permian–Triassic Boundary beds, South China. *Canadian Journal of Earth Sciences* 17(2): 289–295, 2 pls.

LIAO, Z. T., 1984. New genera and species of Late Permian and earliest Triassic brachiopods from Jiangsu, Zhejiang and Anhui Provinces. *Acta Palaeontologica Sinica* 23(3): 276–285, 2 pls. (In Chinese.)

LIAO, Z. T., 1987. Palaeoecological characters and stratigraphic significance of silicified brachiopods of the Upper Permian from Heshan, Laibin, Guangxi. In *Stratigraphy and Palaeontology of Systemic boundaries in China, Permian and Triassic Boundary*, Nanjing Institute of Geology and Palaeontology, Academia Sinica, eds, Nanjing University Press, Nanjing, China, 81–125, 8 pls. (In Chinese.)

MEI, S. L., 1997. Restudy of conodonts from the Permian–Triassic Boundary beds at Selong and Meishan and the natural Permian–Triassic boundary. In *Centennial Memorial Volume of Prof. Sun Yunzhu: Palaeontology and Stratigraphy*, Wang Hongzhen & Wang Xunlian, eds, China University of Geosciences Press, Wuhan, China, 141–148, pls 18.1–2.

MUIR-WOOD, H. M., 1962. *On the morphology and classification of the brachiopod suborder Chonetoidea*, British Museum (Natural History), London, 1–132, 16 pls.

MUIR-WOOD, H. M., 1965. Chonetacea. In *Treatise on Invertebrate Paleontology, Part H, Brachiopoda 1*, R. C. Moore, ed., Geological Society of America and University of Kansas Press, New York and Lawrence, H412–H438.

PAECKELMANN, W., 1930. Die Fauna des Deutschen Unterkarbons 1, Teil, Die Brachiopoden, 1, Teil: Die Die Orthiden, Strophomeniden und Choneten des mittleren und oberen Unterkarbons. *Abhandlungen der Preussischen geologischen Landesanstalt, Neue Folge* 122: 143–326, pls 9–24.

SHENG, J. Z. & JIN, Y. G., 1994. Correlation of Permian deposits of China. *Palaeoworld* 4: 14–113.

SHEN, S. Z., ARCHBOLD, N. W. & SHI, G. R., 1999. Changhsingian (Late Permian) brachiopod palaeobiogeography. *Historical Biology* 14 (in press).

SHI, G. R. & SHEN, S. Z., 1998. A Changhsingian (Late Permian) brachiopod fauna from Son La, northwest Vietnam. *Journal of Asian Earth Sciences* 16: 501–511.

SUESS, E., 1893. Are great ocean depths permanent? *Natural Science* 2: 180–187.

WAAGEN, W. H., 1882–1885. Salt Range fossils: *Productus* Limestone fossils, Pt 4(2): Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologia Indica, Series 13* 4(1–5): 329–770, pls 25–86.

WANG, G. P., LIU, Q. Z., JIN, Y. G., HU, S. Z., LIANG, W. P. & LIAO, Z. T., 1982. Brachiopods. In *Palaeontological Atlas of Eastern China*, Nanjing Institute of Mineralogy and Resources, Geological Academy of China, eds, Geological Publishing House, Beijing, 186–256, pls 74–102. (In Chinese.)

WANG, Y., JIN, Y. G. & FANG, D. W., 1964. *Brachiopod fossils of China*, Science Press, Beijing, 1–777, 136 pls. (In Chinese.)

WANG, Y. G., CHEN, C. Z., RUI, L., WANG, Z. H., LIAO, Z. T. & HE, J. W., 1989. A potential global stratotype of Permian–Triassic boundary. In *Development in Geoscience*, Chinese Academy of Sciences, eds, Science Press, Beijing, 221–228, 1 pl. (In Chinese.)

WATERHOUSE, J. B., 1983. Permian brachiopods from Pija Member, Seaja Formation, in Manang district of Nepal, with new brachiopod genera and species from other regions. *Bulletin, Indian Geologists Association* 16(2): 111–151.

WATERHOUSE, J. B. & PIYASIN, S., 1970. Mid-Permian brachiopods from Khao Phrik, Thailand. *Palaeontographica, Abteilung A* 135: 83–197, 19 pls.

WILLIAMS, A. & BRUNTON, C. H. C., 1997. Morphological and anatomical terms applied to brachiopods. 421–440. In *Treatise on invertebrate paleontology, Part H, Brachiopoda (revised) 1, Introduction*, A. Williams, C. H. C. Brunton & S. J. Carlson, eds, The Geological Society of America Inc. and The University of Kansas, Boulder, Colorado, and Lawrence, Kansas, 539 pp.

XU, G. R., 1987. Brachiopoda. In *Permian–Triassic boundary stratigraphy and fauna of South China*, Z. Y. Yang, H. F. Yin, S. B. Wu, F. Q. Yang, M. H. Ding & G. R. Xu, eds, *Geological Memoirs, Series 2 (Stratigraphy and Palaeontology)* 6: 317–326, pls 7–16, Geological Publishing House, Beijing. (In Chinese.)

XU, G. R. & GRANT, R. E., 1994. Brachiopods near the Permian–Triassic boundary in South China. *Smithsonian Contributions to Paleobiology* 76: 1–68.

YANG, D. L., NI, S. Z., CHIANG, M. L. & ZHAO, R. X., 1977. Brachiopods. In *Palaeontological Atlas of Central-South China. 2*, Geological Publishing House, Beijing, 306–470, pls 129–188. (In Chinese.)

YANG, Z. Y., TING, P. C., YIN, H. F., CHANG, S. X. & FAN, G. C., 1962. The brachiopod fauna of the Carboniferous, Permian and Triassic in the Chi Lianshan Region. *Monograph on the Qilianshan Mountains* 4(4): 1–134, 48 pls, Science Press, Beijing. (In Chinese.)

YIN, H. F., WU, S. B., DING, M. H., ZHANG, K. X., TONG, J. N., YANG, F. Q. & LAI, X. L., 1996. The Meishan section, candidate of the Global Stratotype Section and Point of the Permian–Triassic Boundary. In *The Palaeozoic–Mesozoic Boundary Candidates of Global Stratotype Section and Point of the Permian–Triassic Boundary*, H. F. Yin, ed., China University of Geosciences Press, Wuhan, China, 31–48.

ZENG, Y., HE, X. L. & ZHU, M. L., 1995. *Permian brachiopods and community succession in the Huayin mountains, Sichuan*, China University of Mineralogy Press, Xuzhou, China, 1–187, 21 pls. (In Chinese.)

ZHAN, L. P., 1979. Brachiopods. In *The coal-bearing strata and fossils of Late Permian from Guangtung*, H. F. Hou, L. P. Zhan & B. W. Chen, eds, Geological Publishing House, Beijing, 20–30, pls 4–13. (In Chinese.)

ZHAN, L. P., 1989. Brachiopods. In *Study on the Permian–Triassic biostratigraphy and event stratigraphy of northern Sichuan and southern Shaanxi*, Z. S. Li, L. P. Zhan, J. Y. Dai, R. G. Jin, X. F. Zhu, J. H. Zhang, H. Q. Huang, D. Y. Xu, Z. Yan & H. M. Li, eds, *Ministry of Geology and Mineral Resources, People's Republic of China, Geology Memoir* 2(9): 205–211, pls 25–28. (In Chinese.)

ZHANG, K. X., 1995. Late Permian Changhsingian ecostratigraphy of Lower Yangtze region. In *Dongwuan–Indosinian (Late Permian–Middle Triassic) Ecostratigraphy of the Yangtze Region and its Margins*, H. F. Yin, M. H. Ding, K. X. Zhang, J. N. Tong, F. Q. Yang & X. L. Lai, eds, Science Press, Beijing, 80–95. (In Chinese.)

ZHANG, S. X. (CHIANG, S. X.) & JIN, Y. G. (CHING, Y. K.), 1976. Late Paleozoic brachiopods from the Mountain Jolmo Lungma Region. In *A report of the scientific expedition in the Mountain Jolmo Lungma Region (1956–1958) (Palaeontology)* 2: 159–271, 19 pls, Science Press, Beijing. (In Chinese.)

ZHAO, J. K., SHENG, J. C., YAO, Z. Q., LIANG, X. L., CHEN, C. Z., RUI, L. & LIAO, Z. T., 1981. The Changhsingian and Permian–Triassic Boundary of South China. *Bulletin of the Nanjing Institute of Geology and Palaeontology, Academia Sinica* 2: 1–95, 16 pls. (In Chinese.)